

Mapping out a future for ungulate migrations

Authors: Matthew J. Kauffman¹, Francesca Cagnacci², Simon Chamaille-Jammes^{3,4,5}, Mark Hebblewhite⁶, J. Grant C. Hopcraft⁷, Jerod A. Merkle⁸, Thomas Mueller^{9,10}, Atle Mysterud¹¹, Wibke Peters¹², Christiane Roettger¹³, Alethea Steingisser¹⁴, James E. Meacham¹⁴, Kasahun Abera¹⁵, Jan Adamczewski¹⁶, Ellen O. Aikens^{17,18,19}, Carly Vynne²⁰, Hattie Bartlam-Brooks²¹, Emily Bennett²², Joel Berger^{23,24}, Charlotte Boyd²⁵, Steeve D. Côté²⁶, Lucie Debeffe²⁷, Nandintsetseg Dejid⁹, Emiliano Donadio²⁸, Luthando Dziba²⁹, William F. Fagan³⁰, Claude Fischer³¹, Stefano Focardi³², John Fryxell³³, Richard W.S. Fynn²², Chris Geremia³⁴, Benito A. González³⁵, Anne Gunn³⁶, Elie Gurarie³⁰, Marco Heurich^{37,38}, Jodi Hilty³⁹, Mark Hurley⁴⁰, Aran Johnson⁴¹, Kyle Joly⁴², Petra Kaczensky^{43,44}, Corinne J. Kendall⁴⁵, Pavel Kochkarev⁴⁶, Leonid Kolpaschikov⁴⁷, Rafał Kowalczyk⁴⁸, Frank van Langevelde⁴⁹, Binbin Li⁵⁰, Alex L. Lobora⁵¹, Anne Loison⁵², Tinaapi H. Madiri⁵³, David Mallon^{54,55}, Pascal Marchand⁵⁶, Rodrigo A. Medellin^{13,57}, Erling Meisingset⁵⁸, Evelyn Merrill⁵⁹, Arthur D. Middleton⁶⁰, Kevin L. Monteith⁶¹, Malik Morjan^{62,63}, Thomas A. Morrison⁷, Steffen Mumme^{2,64}, Robin Naidoo⁶⁵, Andres Novaro⁶⁶, Joseph O. Ogutu⁶⁷, Kirk A. Olson⁶⁸, Alfred Oteng-Yeboah^{13,69}, Ramiro J.A. Ovejero^{70,71}, Norman Owen-Smith⁷², Antti Paasivaara⁷³, Craig Packer⁷⁴, Danila Panchenko⁷⁵, Luca Pedrotti⁷⁶, Andy Plumptre⁷⁷, Christer M. Rolandsen⁴³, Sonia Said⁷⁸, Albert Salemgareyev⁷⁹, Aleksandr Savchenko⁸⁰, Piotr Savchenko⁸⁰, Hall Sawyer⁸¹, Moses Selebatso⁸², Matthew Skroch⁸³, Erling Solberg⁴³, Jared A. Stabach⁸⁴, Olav Strand⁴³, Michael J. Sutor⁸⁵, Yasuyuki Tachiki⁸⁶, Anne Trainor⁸⁷, Arnold Tshipa^{88,89}, Munir Z. Virani⁹⁰, Stephanie Ward⁹¹, George Wittemyer²³, Wenjing Xu⁶⁰, Steffen Zuther⁹¹

Affiliations:

¹U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA.

²Department of Biodiversity and Molecular Ecology, Research and Innovation Centre, Fondazione Edmund Mach, 38010 San Michele all'Adige, Italy.

³CEFE, Univ Montpellier, CNRS, EPHE, IRD, Univ Paul Valéry Montpellier 3, Montpellier, France.

⁴Department of Zoology & Entomology, Mammal Research Institute, University of Pretoria, Pretoria, South Africa.

⁵LTSER France, Zone Atelier "Hwange", Hwange National Park, Bag 62, Dete, Zimbabwe.

⁶Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, Franke College of Forestry and Conservation, University of Montana, Missoula, MT, 59812, USA.

⁷Boyd Orr Centre for Population and Ecosystem Health, Institute of Biodiversity, Animal Health & Comparative Medicine (IBAHCM), University of Glasgow, G12 8QQ, UK.

⁸Department of Zoology and Physiology, University of Wyoming, Laramie, WY, 82071, USA.

⁹Senckenberg Biodiversity and Climate Research Centre, Senckenberg Gesellschaft für Naturforschung, Senckenberganlage 25, 60325 Frankfurt (Main), Germany.

- ¹⁰Department of Biological Sciences, Goethe University Frankfurt, 60323 Frankfurt (Main), Germany.
- ¹¹Centre for Ecological and Evolutionary Synthesis, Department of Biosciences, University of Oslo, P.O. Box 1066 Blindern, NO-0316 Oslo, Norway.
- ¹²Bavarian State Institute of Forestry, Department for Conservation, Biodiversity and Wildlife Management, 85354 Freising, Germany.
- ¹³Secretariat of the Convention on the Conservation of Migratory Species of Wild Animals (CMS), 53113 Bonn, Germany.
- ¹⁴InfoGraphics Lab, Department of Geography, University of Oregon, Eugene, OR, 97403, USA.
- ¹⁵German Technical Cooperation (GIZ), Biodiversity and Forestry Programme in Ethiopia. Addis Ababa, Ethiopia.
- ¹⁶Wildlife Division, Environment and Natural Resources, Government of Northwest Territories, Yellowknife, NT, X1A 2L9 Canada.
- ¹⁷Department of Migration, Max Planck Institute of Animal Behavior, 78315 Radolfzell, Germany.
- ¹⁸Department of Biology, University of Konstanz, 78457 Konstanz, Germany.
- ¹⁹Centre for the Advanced Study of Collective Behaviour, University of Konstanz, 78468 Konstanz, Germany.
- ²⁰Osprey Insights, Seattle, WA, 98115, USA.
- ²¹Structure and Motion Laboratory, The Royal Veterinary College, Hatfield AL9 7TA, UK.
- ²²Okavango Research Institute, University of Botswana, Maun, Botswana.
- ²³Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fort Collins, CO 80523, USA.
- ²⁴Wildlife Conservation Society, Bronx, New York, 10460, USA.
- ²⁵International Union for Conservation of Nature (IUCN), North America Office, Washington, DC 20009, USA.
- ²⁶Département de biologie, Caribou Ungava & Centre d'études nordiques, Université Laval, Québec (QC), G1V 0A6, Canada.
- ²⁷Université de Toulouse, INRAE, CEFS, F-31326, Castanet-Tolosan, France.
- ²⁸Fundación Rewilding Argentina, Estancia La Ascensión, Los Antiguos, Santa Cruz 9041, Argentina.
- ²⁹Conservation Services, South African National Parks, Pretoria, 0001, South Africa; Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth, South Africa
- ³⁰Department of Biology, University of Maryland, MD, 20742, USA.
- ³¹University of Applied Sciences of Western Switzerland, Department of Nature Management, 1274, Jussy, Switzerland.
- ³²Istituto dei Sistemi Complessi del CNR, 50019 Sesto Fiorentino, Italy.

- ³³Department of Zoology, Biodiversity Institute of Ontario (BIO), Center for Biodiversity Genomics, University of Guelph, Guelph, Ontario N1G 2W1, Canada.
- ³⁴Yellowstone Center for Resources, Yellowstone National Park, Mammoth Hot Springs, WY 82190, USA.
- ³⁵Laboratorio de Ecología de Vida Silvestre, Facultad de Ciencias Forestales y de la Conservación de la Naturaleza, Universidad de Chile, Santiago, Chile.
- ³⁶Circum-Arctic Rangifer Monitoring and Assessment, Salt Spring Island, British Columbia, V8K 1V1, Canada.
- ³⁷Department of Visitor Management and National Park Monitoring, Bavarian Forest National Park, 94481, Grafenau, Germany.
- ³⁸Chair of Wildlife Ecology and Management, Albert Ludwigs University Freiburg, 79106, Freiburg, Germany.
- ³⁹Yellowstone to Yukon Conservation Initiative, Canmore, AB T1W 1P6, Canada.
- ⁴⁰Idaho Department of Fish and Game, Boise, ID, 83712, USA.
- ⁴¹Southern Ute Indian Tribe, Division of Wildlife Resource Management, Ignacio, CO, 81137 USA.
- ⁴²Gates of the Arctic National Park and Preserve, Arctic Inventory and Monitoring Network, National Park Service, Fairbanks, Alaska, 99709, USA.
- ⁴³Norwegian Institute for Nature Research (NINA), NO-7485, Trondheim, Norway.
- ⁴⁴Research Institute of Wildlife Ecology, University of Veterinary Medicine, Vienna, Austria.
- ⁴⁵North Carolina Zoo Department of Conservation, Education, and Science, 4401 Zoo Parkway, Asheboro, NC, 27205, USA.
- ⁴⁶Central Siberia Nature Reserve "Tsentralnosibirsky", Krasnoyarsk Krai, 648368, Russia.
- ⁴⁷Federal State Budgetary Institution "Reserves of Taimyr", Norilsk, 663305, Russia.
- ⁴⁸Mammal Research Institute, Polish Academy of Sciences, 17-230 Białowieża, Poland.
- ⁴⁹Wildlife Ecology and Conservation Group, Wageningen University and Research, 6708 PB Wageningen, The Netherlands.
- ⁵⁰Environmental Research Centre, Duke Kunshan University, Kunshan, Jiangsu, 215316, China.
- ⁵¹Directorate of Research Development and Coordination, Tanzania Wildlife Research Institute, P.O Box 661, Arusha, Tanzania.
- ⁵²Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LECA, Grenoble, France.
- ⁵³Zimbabwe Parks and Wildlife Management Authority, Hwange National Park, Zimbabwe.
- ⁵⁴Department of Natural Sciences, Manchester Metropolitan University, Manchester M1 5GD, UK.
- ⁵⁵IUCN Species Survival Commission, Gland, Switzerland.

⁵⁶Office Français de la Biodiversité, Direction de la Recherche et de l'Appui Scientifique, Unité Ongules Sauvages, "Les portes du Soleil", F-34990 Juvignac, France.

⁵⁷Instituto de Ecología, Universidad Nacional Autónoma de México (UNAM), 04510 Mexico City, Mexico.

⁵⁸Department of Forestry and Forestry resources, Norwegian Institute of Bioeconomy Research, NO-6630, Tingvoll, Norway.

⁵⁹Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 1Z8, Canada.

⁶⁰Department of Environmental Science, Policy, and Management, University of California, Berkeley, Berkeley, CA 94709, USA.

⁶¹Haub School of Environment and Natural Resources, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82072, USA.

⁶²Ministry of Wildlife Conservation and Tourism, Jebel Lemon, Juba, South Sudan.

⁶³Department of Environmental Studies, School of Natural Resources and Environmental Studies University of Juba, Juba, South Sudan.

⁶⁴Department of Biology and Biotechnologies "Charles Darwin", University of Rome La Sapienza, 00185 Rome, Italy.

⁶⁵WWF-US, 1250 24th Street NW, Washington, DC, 20037, USA.

⁶⁶Instituto de Investigaciones en Biodiversidad y Medioambiente (INIBIOMA)-Consejo Nacional de Investigaciones Científicas (CONICET)-Universidad del Comahue and Wildlife Conservation Society-Argentina, 8371 Neuquén, Argentina.

⁶⁷Biostatistics Unit, Institute of Crop Science, University of Hohenheim, 70599 Stuttgart, Germany.

⁶⁸Wildlife Conservation Society, Mongolia Country Program, Ulaanbaatar-14200, Mongolia.

⁶⁹Council for Scientific and Industrial Research - Ghana, Wildlife Division, Forestry Commission of Ghana, Accra, Ghana.

⁷⁰Instituto de Ecología Regional (IER), Universidad Nacional de Tucumán (UNT)-Consejo Nacional de Investigaciones Científicas (CONICET), CCT-CONICET-TUCUMAN, Tucumán, Argentina.

⁷¹Laboratorio de Ecología Conductual, Instituto de Ciencias Ambientales y Evolutivas, Facultad de Ciencias; Universidad Austral de Chile (UACH)-Comisión Nacional de Investigación Científica y Tecnológica (CONICYT), Valdivia, Chile.

⁷²Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Wits, 2050 South Africa.

⁷³Natural Resources Institute Finland, FI-00790, Helsinki, Finland.

⁷⁴Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108, USA.

- ⁷⁵Institute of Biology of the Karelian Research Centre of the Russian Academy of Sciences, 185910 Petrozavodsk, Russia.
- ⁷⁶Stelvio National Park, 23032 Bormio (SO), Italy.
- ⁷⁷Key Biodiversity Area Secretariat, BirdLife International, Cambridge CB2 3QZ, UK.
- ⁷⁸Office Français de la Biodiversité, Direction de la Recherche et de l'Appui Scientifique, "Montfort", 01330 Birieux, France.
- ⁷⁹Association for the Conservation of Biodiversity of Kazakhstan (ACBK), Nur-Sultan, 010000 Kazakhstan.
- ⁸⁰Department of Wildlife Resource Studies and Reserve Management, Institute of Ecology and Geography, Siberian Federal University, 660041, Krasnoyarsk, pr. Svobodnyi, Russia.
- ⁸¹Western EcoSystems Technology, Inc., Laramie, WY, 82072, USA.
- ⁸²Kalahari Research and Conservation Trust, Gaborone, Botswana.
- ⁸³The Pew Charitable Trusts, Portland, OR, 97201, USA.
- ⁸⁴Smithsonian National Zoo & Conservation Biology Institute, Conservation Ecology Center, Front Royal, VA 22630, USA.
- ⁸⁵Fish and Wildlife Branch, Environment Yukon, Government of Yukon, Dawson City, Yukon, Y0B 1G0, Canada.
- ⁸⁶Rakuno Gakuen University, 069-8501 Ebetsu, Hokkaido, Japan.
- ⁸⁷The Nature Conservancy, Africa Program, Cincinnati, OH 45221, USA.
- ⁸⁸Wilderness Safaris, Victoria Falls, Zimbabwe.
- ⁸⁹Department of Forestry Resources and Wildlife Management, National University of Science and Technology, Ascot, Bulawayo, Zimbabwe.
- ⁹⁰The Peregrine Fund, Boise, ID 83709, USA.
- ⁹¹Frankfurt Zoological Society, Altyn Dala Conservation Initiative, 60316 Frankfurt am Main, Germany.

*Correspondence to: mkauffm1@uwyo.edu.

Main Text:

Wildebeest, 1.3 million strong, plod steadily across the Serengeti plains, chasing the recent rains. Hundreds of thousands of caribou crisscross the Arctic, their hooves pounding across the vast tundra. A mule deer doe pauses along her two-month march to nibble the green grass of spring before rejoining a well-worn trail through the sagebrush. The migrations of ungulates (hooved mammals) are some of the most impressive phenomena in the animal kingdom. And while millions of people have observed some of these journeys, such as the wildebeest migration, animal tracking studies are discovering new ungulate migrations that surprise scientists and the public alike.

Migration is a fundamental ecological process that promotes abundant herds (1), whose biomass cascades up and down terrestrial food webs. Migratory ungulates provide the prey base that maintains large carnivore and scavenger populations and underpins terrestrial biodiversity. When ungulates move in large aggregations, their hooves, feces and urine create conditions that facilitate unique biotic communities (2). The phenomenon of migration thus provides a wealth of ecosystem services, while also supporting indigenous people and local communities on many continents. More than just using them for food and clothing, humans have been culturally linked to and sustained by migratory ungulates for thousands of years.

Despite their importance, ungulate migrations are disappearing at an alarming rate (3). Without a strategic and collaborative effort, many of the world's great migrations will continue to be truncated, severed, or lost in the coming decades. Fortunately, an evidence-based alternative exists. A combination of indigenous knowledge, historical records, animal tracking datasets, and

analytical tools can provide the information necessary to conserve ungulate migration. Through our collective efforts to study the world's ungulate migrations, we recognize an urgent need for a global inventory of known migrations, including those extant and recently lost.

New Technology, New Discoveries

Ungulates migrate in response to resources that wax and wane with the seasons. In the tropics, species like kob, eland, and elephant track rainfall across vast grasslands in search of food or water. In temperate systems, many ungulates move between mountains and plains to escape the deep snows of winter and feed on high-quality forage in summer. Across the Arctic, migratory caribou and reindeer move hundreds of kilometers from the boreal forests across the snow-covered tundra to aggregate on their northern calving grounds just as plants are greening up. The sheer numbers of caribou on the calving grounds dilutes the toll from their wolf, bear and wolverine predators (4).

Powerful new methods have made it possible to map migrations with precision. Tracking devices that are small, affordable, and reliable are being deployed on many species, allowing movement data to be acquired hourly at ~10-meter resolution. Satellites can now provide remotely sensed data to characterize spring green-up, drought, or snow, at the same scale migrating animals make behavioral decisions. When animal tracks are overlaid on dynamic maps of the earth's seasonal resources they reveal diverse migratory behaviors, from long-distance movements across climatic gradients, to shorter elevational movements to access alpine habitats.

Recent discoveries span several continents. In 2014, a zebra migration was discovered that stretches 500 km across Namibia and Botswana, a new record for the species (5). In 2016, in the

Greater Yellowstone Ecosystem, mule deer were found to travel as far as 400 km one way (6). On the Mongolian Steppe, gazelle were found in 2018 to explore an area roughly the size of Hungary (100,000 km²) over their lifetime (7). Most recently, in Ethiopia's Gambella National Park, researchers discovered that white-eared kob migrate in an 860 km circuit connecting to the Boma-Bandingilo migration in South Sudan, extending the known migratory range (8). Altitudinal migrations are also being revealed across the world's mountain ranges. These short migrations allow animals to exploit highly variable habitats and derive functional benefits similar to long-distance migrations.

There is growing recognition that migratory behavior must be learned by mammals. In North America for example, migratory bighorn sheep and moose failed to migrate when first translocated into novel landscapes. Over multiple generations, however, individual populations gained knowledge to move and find forage, and they became more migratory (9). Sustained by spatial memory, migratory behavior may often exist as a type of animal culture that must be learned and transmitted between generations. The reliance on culture carries a stark warning for conservation, namely that the persistence of a given migration corridor depends on the survival of individuals that possess the knowledge to make it.

Migrations in Danger

The world's landscapes are changing rapidly, and unlike migratory birds, ungulates cannot fly over patches of unsuitable habitat. Instead, they must share the landscape with humans, making them especially vulnerable to land-use changes that impede their movements. Recent estimates project that we will build 25 million km of new roads across the globe by 2050 (10), with

associated constraints on animal movement. The sheer scale of these developments casts a long shadow over the future of terrestrial migrations.

Impermeable barriers have long restricted the free movement of migratory herds. For example, nomadic movements of Mongolian gazelles are now constrained by railroads and border fences (7). In Botswana, veterinary fences built in the 1950s caused the death of hundreds of thousands of wildebeest. In the western U.S., highways have severed pronghorn and mule deer migrations (11). In Russia's Kola Peninsula, the construction of a railroad divided the wild reindeer population and eliminated the longest of the region's migrations. And in Europe, red deer must navigate a landscape shaped by centuries of human settlement, exploiting seasonal cycles of forage only in the most remote habitats.

Semipermeable barriers like unfenced roads, some fences, dwellings, and energy extraction are also increasing. Although animals may be able to pass through such impacted landscapes, their altered movements are often mismatched with patterns of rainfall or snowmelt. In the most extreme cases, migrations can be lost simply because the costs of navigating human-altered landscapes outweigh the benefits of migrating.

Climate change is an additional challenge. Many ungulates time their migrations to exploit patterns of plant green-up. Droughts are becoming commonplace, making it more difficult for animals to move in synchrony with green-up and access the best forage (12). Migratory ungulates are thus doubly challenged by a changing climate combined with barriers that prevent them from adjusting their movement tactics as conditions change. Protected areas rarely ease

these challenges, because they remain too small to maintain the full sweep of resources needed to sustain most long-distance migrations.

Past landscape changes have taken their toll on ungulate migrations. Harris et al. (3) in 2009 described the loss of six out of 24 ungulate populations that make mass migrations. Historical accounts describe numerous migrations that no longer exist in the behavioral repertoire of current populations. The hundreds of thousands of Cape springbok that once traversed the Karoo landscape of South Africa were eradicated by fencing, disease, and hunting at the end of the 19th century. In Kenya's Kajiado County, migrations of wildebeest, zebra and Thomson's gazelle have collapsed due to competition with livestock and massive land conversion. When we lost the tens of millions of bison that roamed North America, we lost the abundance necessary to sustain migration (2). Of the bison that now exist in small conservation herds, the Yellowstone population is one of a few that migrate.

When we lose the large herds of animals moving *en masse* across the landscape, we lose something else even more difficult to quantify. Such phenomena, the thundering of hooves kicking up dust as a herd moves across a vast landscape, remind us of the wildness that the Earth's habitats are still capable of supporting. Equally important are the cultural traditions and identity of many indigenous communities, such as the Inuit and Tlicho, whose livelihoods depend on migratory herds (13).

The movements of ungulates across the globe are more diverse and behaviorally complex than previously recognized. To maintain this diversity of movement, conservation of corridors and

landscape connectivity has taken on new urgency. Unfortunately, efforts by wildlife managers and conservationists are thwarted by a singular challenge: Most ungulate migrations have never been mapped in enough detail to guide effective conservation.

A Conservation Solution

New methods now allow corridors to be mapped in detail from tracking data (14). When maps are overlaid on real landscapes, barriers and other threats can be identified, pointing the way to effective solutions. Migration maps are increasingly being used to target fences for removal, site overpasses and underpasses, guide energy leasing, and prevent housing development from blocking corridors. For species with high fidelity to corridors, such as mule deer (6), conservation may be achieved by targeted planning within corridors. For species that make nomadic or variable migrations, such as red deer, Mongolian gazelle, khulan, and barren-ground caribou, broader-scale strategies are needed to map and conserve their annual migrations and seasonal ranges. Regardless, mapping efforts to date illustrate that empirical tracking data can effectively guide efforts to conserve migrations.

We also need to inventory and map migrations that have already been lost, which is possible through indigenous, local, and expert knowledge. Mapping lost migrations can provide an important benchmark from which we can push back shifting baselines. For example, after a veterinary fence in Botswana that had blocked movements for 36 years was removed, zebra were recorded in 2004 making a nearly 600-km round trip migration similar to the one described in reports of historical sightings (15). In some South American rangelands, conservationists are hopeful that ranch abandonment will create opportunities to restore lost migrations of guanacos

and huemul deer. We don't know which migrations can be restored, but mapping where they once existed is a necessary first step.

The Convention on Migratory Species (CMS) advanced conservation by formally recognizing animal migrations in 1979. Yet, tracking data have not existed in sufficient detail to map ungulate migrations until recently, which has constrained Parties to the Convention from developing concrete policies to protect migrations. We therefore propose a global atlas of ungulate migration, built from new and existing tracking studies. We envision a digital archive that translates tracking data into actionable migration maps that are standardized, in a central database, and publicly available. The atlas would be a resource for multiple stakeholders, such as indigenous peoples, local, regional, or national governments, and NGOs, to collaboratively manage shared landscapes to sustain known migrations while maintaining local livelihoods. Such an evidence-based effort is needed to assure that migrations – the actual paths that herds have used for hundreds or thousands of years – are incorporated into land management plans, environmental impact assessments, mitigation activities, and reserve designs. The atlas will also facilitate international coordination to protect transboundary movements and inform the development work of International Finance Institutions.

This will require dedicated collaboration on a global scale. Fortunately, tracking datasets are growing each year, and existing data can be analyzed now to begin an archive of detailed migration maps. Migrations that remain unmapped can be targeted for new field studies. To coordinate this effort, we have created the Global Initiative for Ungulate Migration (GIUM). The GIUM brings together scientists, conservationists and wildlife managers around the world to

create a collaborative knowledge base of ungulate migrations, develop a global atlas, and spark new conservation and policy.

No doubt current and future generations will continue to be amazed by the annual treks of wildebeest across the Serengeti. We must now turn our research and conservation efforts to other species, such as the saiga and khulan in central Asia, the Arctic caribou and reindeer across North America and Eurasia, the moose in Scandinavia, and the guanaco and huemul in South America, to name just a few. Such an ambitious atlas brings hope that new migration maps can guide where we build roads, fences, and other infrastructure, and where we decide to forego such developments to safeguard the movement of animals. Through global collaboration, we can now assemble the knowledge, data, and tools necessary to maintain the wild and intact landscapes that migratory ungulates require and sustain the ecosystems supported by their abundance.

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Migration underpins terrestrial ecosystems

The annual migration of 1.3 million wildebeest, plus several hundred thousand zebra, gazelle, and eland, influence ecological dynamics in the Serengeti ecosystem, including positive feedback loops on grassland productivity. This mass migration of herbivores supports a diverse predator and scavenger community that tracks their year-round movements.

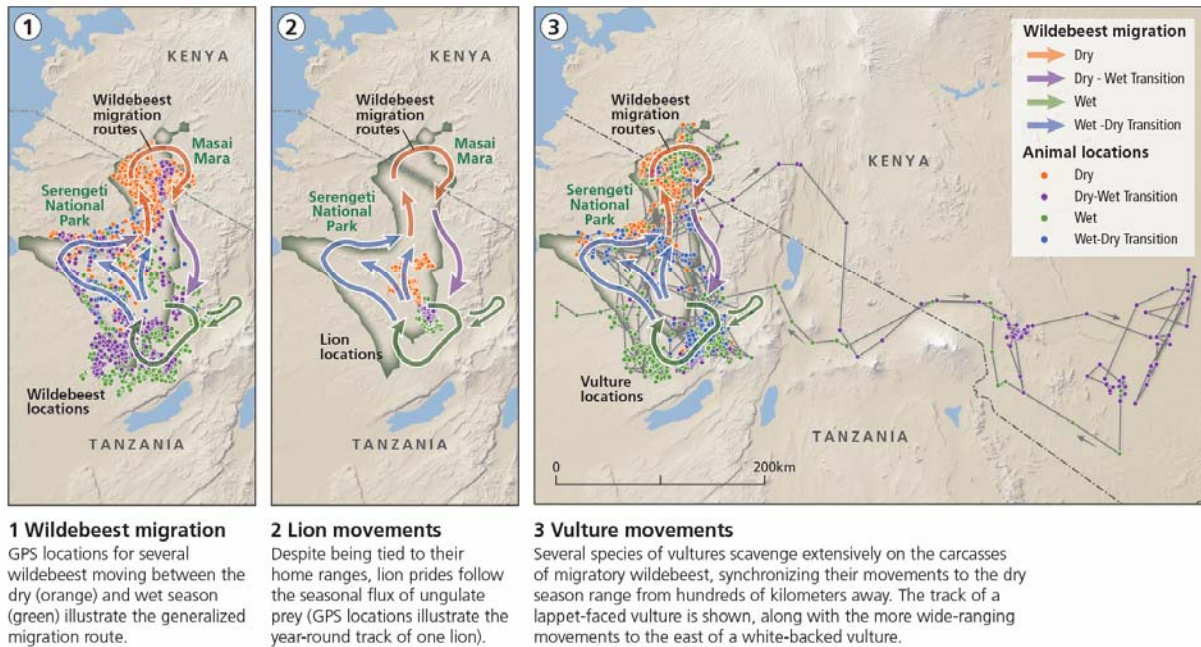


Fig. 1. Migration underpins terrestrial ecosystems. The annual migration of 1.3 million wildebeest, plus several hundred thousand zebra, gazelle, and eland, influence ecological dynamics in the Serengeti ecosystem, including positive feedback loops on grassland productivity. This mass migration of herbivores supports a diverse predator and scavenger community that tracks their year-round movements.

1. Wildebeest migration

GPS locations for several wildebeest moving between the dry (orange) and wet season (green) illustrate the generalized migration route.

2. Lion movements

Despite being tied to their home ranges, lion prides follow the seasonal flux of ungulate prey

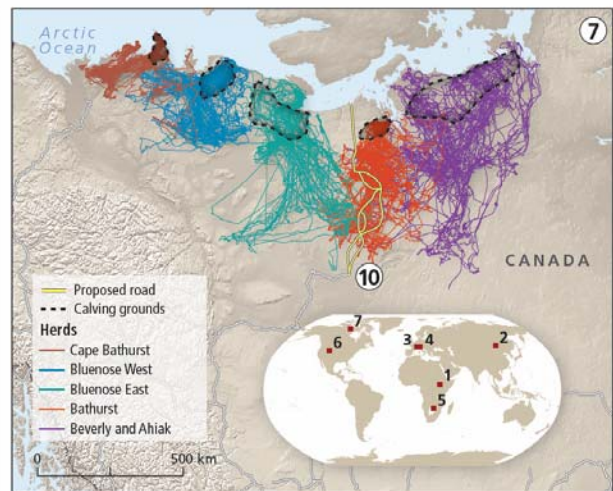
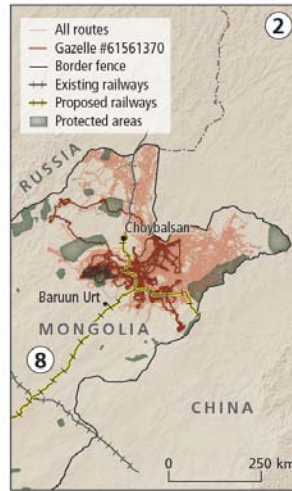
(GPS locations illustrate the year-round track of one lion).

3. Vulture movements

Several species of vultures scavenge extensively on the carcasses of migratory wildebeest, synchronizing their movements to the dry season range from hundreds of kilometers away. The track of a lappet-faced vulture is shown, along with the more wide-ranging movements to the east of a white-backed vulture.

Ungulate migrations around the world

Animal tracking studies are being conducted around the world, facilitating discovery of previously unknown movements and making it possible to map migration and identify threats with precision.



1 White-eared kob

In 2018, white-eared kob were discovered to make an 860-km migratory circuit between Ethiopia and South Sudan, extending the known migratory range (8). The herds traverse oil and gas concessions, hotspots of armed conflict, and commercial agricultural developments in the Boma-Gambella landscape.

2 Mongolian gazelle

On the Central Asian steppe, the nomadic movements of Mongolian gazelle are an order of magnitude larger than the region's protected areas.

3 Red deer, European Alps

In remote habitats, red deer are still able to fully exploit the abundance of seasonal forage by migrating across mountain ranges.

4 Red deer, semi-urban

Animals living near human population centers may try to maintain migration, but their movements are often constrained and truncated by human settlements.

5 African elephants

Elephants leave Botswana and make a transboundary migration across unprotected areas to find permanent surface-water in their dry season range in Zimbabwe.

6 Wyoming mule deer

A 242-km mule deer migration was discovered in Wyoming in 2014, traversing a mix of public and private lands.

7 Barren-ground caribou

In the Northwest Territories and Nunavut, caribou range over vast areas of Arctic tundra and boreal forest before converging to give birth on herd-specific calving ranges near the coast.

8 A proposed railroad

The annual movements of Mongolian gazelle are bound by impermeable border fences with Russia and China. A proposed railroad threatens to further constrain their large nomadic movements.

9 Oil and gas development

Researchers analyzed tracking data (14) to delineate a high-use corridor (dark blue) from individual routes (orange). The corridor was formally designated by State wildlife officials in 2016, allowing the corridor to be considered during recent oil and gas leasing decisions.

10 A proposed road

Migration tracking data is being used to evaluate proposed alternatives for an all-season road (yellow line) that would cut through the post-calving, summer and winter range of the Bathurst herd, which has declined 97.5% since 2000.

Fig. 2. Ungulate migrations around the world. Animal tracking studies are being conducted around the world, facilitating discovery of previously unknown movements and making it possible to map migration and identify threats with precision.

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Fig. 3. A group of pronghorn pause during their spring migration to navigate a fence that bisects their migration corridor (photo by Joe Riis).

